A STUDY OF EQUILIBRIUM IN THE SMOOTH DOG-FISH—GALEUS CANIS (MITCHILL).*

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Sewell (1882) maintained it would be a bold assumption to assume the semicircular canals, ampullæ and vestibule (utricle and saccule(indispensable to the equilibrium of the selachians. Steiner (1886–1888) stressed the dispensability of these organs; Lee (1884–1886 contended their indispensability. Gaglio (1901) after bilateral ablation of a large part of the labyrinth obtained little or no disturbance of equilibrium. J. Loeb (1891) obtained disturbance of equilibrium following removal of the otolith from one saccule. G. H. Parker (1909) observed no disturbance following removal of the otolith from one or both saccules; section of both acoustic nerves caused profound disturbance of equilibrium. S. S. Maxwell (1910–1923) has observed that the animal swims quite normally after section of the two eighth nerves or after destruction of the two labyrinths. In the teleosts, Tomascewicz (1877) observed no disturbance of equilibrium after destruction of the semicircular canals and their ampulæ; Kiesselback (1882) cutting the horizontal canals on both sides obtained similar negative results.

In this paper we report our observations concerning the equilibrium of the *Galeus Canis* when the selachian was subjected to (1 Bilateral sectioning of the olfactory tracts,

(2) Bilateral sectioning of the optic nerves,
(3) Bilateral destruction of the labyrinths,
(4) Bilateral sectioning of the olfactory tracts, bilateral sectioning of the optic nerves and bilateral destruction of the labyrinths.

The animals were operated without the employment of local or general anæsthesia. Special care was taken to operate while the

* This investigation was undertaken at the U. S. Marine Laboratory, Woods Hole.

animal's head and gills remained submerged in sea water. The animal was fastened to a cork board tilted at an angle of 45° in a large dissecting pan provided with a continuous flow of sea water.

The behavior of the animals was studied in an aquarium 2¼ meters in length, 1¼ meters in width, and ⅘ meter in depth.

The experiments were limited to animals measuring 50 cm. to 75 cm. in length.

Operations.

Sectioning of the Olfactory Tracts.—Part of the cranial encasement (prefrontal and frontal regions) covering the olfactory tract and olfactory lobe was removed. A cavity was exposed which permitted sectioning of the tract. After sectioning the tract, the cavity was filled with cotton. The cotton was held in place by means of drawing stitches at right angles to each other immediately above it. No skin flap was made.

Sectioning of the Optic Nerves.—Cutting through the roof of the mouth a rectangular flap consisting of cartilage and palatal epithelium was made immediately over the junction (chiasma) of the optic nerves. The optic nerves were sectioned 1 mm.–1½ mm. from their place of junction. The flap was sutured into place again.

Destruction of the Labyrinths.—The approach to the labyrinth was made through the roof of the otic capsule. The destruction involved removal of the membranous vestibule (utricle and saccule, the three membranous semicircular canals and the three membranous ampullæ. The cartilaginous labyrinth corresponding to these parts of the membranous labyrinth was lacerated. The resulting cavity was thoroughly cleansed with cotton. After the cleansing, the cavity was filled with a cotton pack and the skin flap made over the roof of the capsule at the beginning of the operation was replaced and sutured.

Experiments and Results.

Bilateral Sectioning of the Olfactory Tracts.—Sectioning both olfactory tracts in the same animal caused no disturbance of equilibrium. Swimming remained normal. The animal died five to

six days after sectioning of the tracts. Six animals were operated upon.

Bilateral Sectioning of the Optic Nerves.—In the same animal, both optic nerves were sectioned. In two cases, swimming remained normal; in five cases movement in the horizontal plane was disturbed. In the latter cases, the animal at times swam around the dorso-ventral axis in circles or in the path of a curved line. Changing the direction of the animal changed the direction of its swimming. Turned to the right, the animal swam to the right around the dorso-ventral axis; turned to the left, it swam to the left. In other planes, the animal swam normally. Twelve to fifteen hours after sectioning of the nerves, the tendency to swim around the dorso-ventral axis disappeared; movement was normal in all planes. The animal died three to four days after the operation.

Bilateral Destruction of the Labyrinths.—In the same animal both labyrinths were carefully and neatly destroyed. In all cases, disturbances of equilibrium resulted. All animals died within three days. The cases may be grouped as follows:

1. Cases (6) in which movement was defective in the vertical and oblique planes to the surface of the water. In other planes, movement was normal. Rotation around the longitudinal axis when swimming in a plane vertical or oblique to the surface of the water never disappeared; it continued until the animal died.

2. Cases (14) in which the animal manifested unsteadiness in keeping the dorsal side up and difficulty in righting itself if placed on its back. The animal swam normally in all planes. At times its ability to keep the dorsal side up becoming critical, the animal would make a turn to the right or to the left towards the bottom of the aquarium. By so doing, it controlled its equilibrium and swam away normally—dorsal side up. Placed ventral side up at the surface of the water, the animal swam on its back a considerable length of time before righting itself. The righting movements were difficult. After a lapse of twenty-four hours, the tendency to be occasionally unsteady in keeping the dorsal side up disappeared; the animal continued to right itself with difficulty when placed on its back.

3. Cases (19) in which the animal retained temporary control

of equilibrium. At times, the animal swam normally in all planes; at other times it lost complete control of its equilibrium. When equilibrium was lost, the animal swam on its back, rotated around its axes, spiraled through the water and nose dived. Rotation around the axes and spirals were made indiscriminately to the right and left. After a period of disturbed equilibrium, the animal regained normal equilibrium only to lose it again sooner or later. The periods of normal and disturbed equilibrium were equally divided. Four to twenty-four hours after destruction of the labyrinths, movement was normal in all planes but if placed ventral side up at the surface of the water the animal swam on its back until it righted. In this respect, equilibrium remained disturbed.

4. Cases (11) in which the animal did not retain temporary control of equilibrium. Following the destruction of the labyrinths, equilibrium was lost for a period of four to twenty-four hours. Movement was disturbed in all planes. As in the case of the preceding group, the animal rotated around its axes, spiraled through the water, swam on its back and nose dived. Twenty-four hours after removal of the labyrinths, movement was normal in all planes. The animal's equilibrium was comparable to the equilibrium of the normal animal but for one exception. Placed ventral side up at the surface of the water, the animal righted itself with difficulty; it swam on its back until it righted. The difficulty in righting itself when placed on its back was always present; it did not disappear.

Bilateral Sectioning of the Olfactory Tracts, Bilateral Sectioning of the Optic Nerves and Bilateral Destruction of the Labyrinths.—In each animal both olfactory tracts, both optic nerves and both labyrinths were destroyed. The olfactory tracts were sectioned first. Two hours later the optic nerves were sectioned. When sectioning of the optic nerves caused the animal to rotate in circles or in the path of a curved line around the dorso-ventral axis, the labyrinths were destroyed after movement in the horizontal plane had become normal. When sectioning of the optic nerves permitted movement in the horizontal plane to remain normal, the labyrinths were destroyed four hours after sectioning of the nerves. The disturbances of equilibrium following destruction of the labyrinths were the same as the disturbances described

when only the labyrinths were destroyed; the improvements in the animal's movements following the disturbances of equilibrium were also the same. In brief, the same types of case were obtained when the destruction of the labyrinths was preceded by sectioning of the olfactory tracts and optic nerves as when only the labyrinths were destroyed. Nineteen animals were operated upon. In four cases, the animal rotated around the longitudinal axis when swimming to the surface of the water; in three cases, the animal manifested unsteadiness in keeping the dorsal side up and difficulty in righting itself when placed on its back; in seven cases, temporary control of equilibrium was retained; in four cases, equilibrium was lost for a period of four to twenty-four hours.

Conclusions.

1. *Bilateral Destruction of the Labyrinths Causes Disturbances of Equilibrium in All Animals.*—In some animals the disturbance is more marked than in others. When the disturbance is not very marked, the animal either rotates around its longitudinal axis when swimming to the surface of the water or swims on its back and rights itself with difficulty when placed ventral side up; when the disturbance is very pronounced the animal rotates around the longitudinal, transverse and dorso-ventral axes, nose dives, spirals, and swims on its back.

2. Allowing the factor of time to intervene, the animals which suffer profound disturbances of equilibrium—such as rotation around the axes, spirals and nose diving—regain most of their equilibrium within twenty-four hours. The animal swims normally in all planes, but if placed ventral side up, it swims on its back and rights itself with difficulty.

3. After sectioning the olfactory tracts or the optic nerves, the animal's equilibrium remains normal. Movement to the right or left around the dorso-ventral axis during the first hours following the sectioning of the optic nerves can not be accepted as disturbance of equilibrium because changing the direction of the animal changes the direction of its swimming.

4. Destruction of the labyrinths after sectioning of the olfactory tracts and optic nerves disturbs the animal's equilibrium similarly as the destruction of the labyrinths alone.

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